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Studies on the Paleozoic Selachian Genus *Ctenacanthus* Agassiz. No. 3. Nominal Species Referred to *Ctenacanthus*

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ABSTRACT

All known nominal species of the Paleozoic chondrichthyan genus *Ctenacanthus* are listed, together with information concerning provenance, whereabouts of type material (where known), important subsequent references and comments on the probable affinities of each species. Other references to undetermined *Ctenacanthus* spp. are listed chronologically. Of some 100 species, 10 are considered totally invalid; the holotypes of five others are known to be lost or destroyed; four others are founded on inadequate material; 10 are referred to the Acanthodii; eight are referred to

another spine genus, *Acondylacanthus*; three are referred to *Asteroptychius*; nine are referred to *Sphenacanthus*; 20 are referred to various other genera; eight are considered close to *Ctenacanthus* but are excluded from it; and 23 are left in *Ctenacanthus*. Of the latter, however, eight are probably synonyms of the type species, *C. major*, and consequently only 15 species are retained. Of these, seven are from the Upper Devonian and eight are from the Lower Carboniferous; all are from marine strata. This stratigraphic range is much less than the previous records have suggested.

INTRODUCTION

In the two preceding parts of this series (Maisey, 1981, 1982), the diagnosis of *Ctenacanthus* has been refined to agree with the type species, *C. major*, and a list of species founded on finspines similar to those of *C. major* has been published. Certain other finspines, differing strongly from those of *C. major*, were referred to various genera in part two of these studies. Many additional forms remain to be surveyed, and it is hoped that some of these will be reviewed in the near

future. In the meantime, it seems advisable to publish a compilation of data concerning prior references to *Ctenacanthus* finspines. The checklist and references given below represent the majority of published accounts. Although I have tried to make this list as complete as possible, perhaps it is inevitable that a few sources have escaped notice. Nevertheless, no similar listing has been compiled since the publication of the second volume of Woodward's (1891) Catalogue, and the

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present compilation may therefore be useful to paleontologists, zoologists, and biostratigraphers. Where the location of a type specimen is known, it is given, together with its catalogue number. Where this datum is absent, the whereabouts of the type material is unknown (although this does not necessarily mean that it is lost, only that I have not been able to locate it). In order to increase the usefulness of the data, notes have been added after each species is listed, and the affinities and validity of the species are discussed. Species of *Ctenacanthus* are listed in alphabetical order, and are followed by a list of indeterminate references to "*Ctenacanthus* sp."

I stress that, while many species have been referred to *Ctenacanthus*, only a small number are based on finspines that compare closely with the type species. Many of the species herein have subsequently been referred to other genera, and probably even more of them will be removed as work progresses. The reader is cautioned here, and is reminded in text, that some of these spines may pertain to very different fishes from *Ctenacanthus*. For diagnoses and discussions of the genus, the following are the main sources: Agassiz (1837), McCoy (1855), Newberry (1873), De Koninck (1878), Davis (1883), Woodward (1891), Eastman (1902, 1907), Obruchev (1967), Maisey (1981, 1982).

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History
BM(NH), British Museum (Natural History)
CNIGR, Central Scientific Research, Geological
Prospecting Museum, Leningrad
MCZ, Museum of Comparative Zoology, Harvard
University
USNM, National Museum of Natural History,
Smithsonian Institution, Washington, D.C.
YPM, Yale Peabody Museum

ALPHABETICAL LIST OF SPECIES

All the following species have been referred to *Ctenacanthus*, in most cases by the original author, but occasionally by a subsequent one. The name is given, followed by the author, reference date, page and illustration numbers. If known, the type specimen is listed, with locality data if any. Additional data are then given under Comments.

Ctenacanthus abnormis Giebel (1858, p. 264, pl. 1, fig. 12).

Lower Devonian, Harz Mountains.

COMMENTS: See also Barrande (1872, p. 628), Kayser (1878, p. 3, Taf. 1, fig. 19). Referred to *Machaeracanthus* by Woodward (1891, p. 123).

Ctenacanthus acutus Eastman (1897), p. 12, fig. 2).

Type specimen, USNM 4683; Mississippian, Keokuk Limestone, Iowa.

COMMENTS: Another specimen, USNM 4682 may be referred to this species. In transverse section and ornamentation pattern *C. acutus* finspines resemble those of *Tristychius*. USNM 3480 said to be close to *C. acutus* (Eastman, 1902, p. 83).

Ctenacanthus aequistriatus Davis (1879a, p. 185, pl. X, fig. 5).

Lower Coal Measures (Pennsylvanian), Yorkshire, England.

COMMENTS: This form was subsequently referred to the genus *Sphenacanthus* by Woodward (1889, p. 244) and Maisey (1982).

Ctenacanthus amblyxiphias Cope (1891, p. 449, pl. XXVIII, fig. 3).

Type specimen, AMNH 7289, Permian, Texas.

COMMENTS: Other references include Eastman (1903), Woodruff (1906), Hussakof (1908, 1911), Branson (1916), Romer (1942), Wells (1944), Berman (1970), and Zidek (1976). According to Wells (1944), however, Eastman's (1903) finspine is closer to that of *C. lamborni*; this is also the case with Branson's (1916) specimen.

Ctenacanthus angulatus Newberry and Worthen (1866, p. 118, pl. XII, fig. 4).

Type specimen, University of Illinois X-1152, Mississippian, Chester Limestone, Chester, Illinois.

COMMENTS: There are similarities between *C. angulatus* and *C. similis* finspines, but these are not sufficient to suggest synonymy. *Ctenacanthus angulatus* is among the species retained in the genus by Maisey (1981).

Ctenacanthus angustus Newberry (1889, p. 181).

Type specimen, AMNH 5269, "Subcarboniferous," Berea Grit, Berea, Ohio.

COMMENTS: The type was not figured by Newberry (1889) but the specimen so designated bears a label in his handwriting. A detail of its ornament was subsequently figured (Hussakof, 1908, fig. 19). The species is among those retained in the genus by Maisey (1981). Some specimens referred to "*C. angustens*" e.g., BM(NH) P9581, P9262, may pertain to this species.

Ctenacanthus bellus Branson (1906, p. 1393, pl. XLII, figs. 19–21).

Syntypes, AMNH 6446 (two pieces), Mississippian, Salem Limestone, Lanesville, Indiana.

COMMENTS: This species is not referable to *Ctenacanthus*. The wedge-shaped transverse section, tubercles toward the leading edge, and presence of a narrow median ridge posteriorly characterize this as an *Asteroptychius* fin spine.

Ctenacanthus bohemicus Barrande (1872).

Lower Devonian (Siegenian), Lochkov Limestone (Bohemia), Taunusquartzit (Rheinland).

COMMENTS: Referred to *Machaeracanthus* by Woodward (1891, p. 124), Fritsch (1895, p. 72), and Denison (1979, p. 52); probably an acanthodian.

Ctenacanthus bosnensis Katzer (1916, p. 201, Tab. 1, figs. 1–13),

Triassic, near Sarajevo, Bosna i Hercegovina, Yugoslavia.

COMMENTS: This species is probably referable to *Nemacanthus*. Its fin spines are characteristically ornamented with longitudinal series of rounded tubercles laterally and an enameled keel anteriorly.

Ctenacanthus brevis Agassiz (1837, vol. III, p. 11, table 2, fig. 2).

Type specimen, Bristol City Museum C4154, Mississippian, Carboniferous Limestone (Avonian, Z₂ fishbeds), Clifton, near Bristol, England.

COMMENTS: Agassiz (1837) figured a drawing rather than the specimen, which he had not seen prior to publication. The type specimen is figured in Maisey (1982, fig. 2). Another specimen, BM(NH) 3111-2, was described and figured by Davis (1883, p. 337, pl. XLIII, fig. 3). The species is removed from

Ctenacanthus and referred instead to *Bythiacanthus* by Maisey (1981, 1982). Several other specimens were listed by Woodward (1891, p. 100), who noted that *C. limaformis* is probably synonymous with this species.

Ctenacanthus browni Branson (1916, p. 653, pl. IV, fig. 7, text fig. 6).

Type specimen, University of Missouri no. 709, Upper Carboniferous, Embar Formation, Wyoming.

COMMENTS: An additional specimen was referred to the species by Branson (1933). The fin spine was not included in *Ctenacanthus* by Maisey (1981); it is more probably allied to *Acondylacanthus*.

Ctenacanthus burlingtonensis St. John and Worthen (1875, p. 426, pl. XV, figs. 6, 7).

Cotypes, USNM 13523 and 13524, Mississippian, St. Louis Limestone, St. Louis, Missouri.

COMMENTS: An additional specimen, AMNH 1031, seems close to the type material in many respects. The fragments upon which this species is based are remarkably similar to fin spines of *Acondylacanthus gracillimus*. Probably *C. burlingtonensis* is synonymous with *C. gradocostus*.

Ctenacanthus buttersi St. John and Worthen (1883, p. 240, pl. XXII, fig. 2).

Pennsylvanian, Lower Coal Measure, Carlinville, Illinois.

COMMENTS: The ornamentation of the type specimen differs from that of *Ctenacanthus* fin spines. The general shape and the arrangement of the ornament in *C. buttersi* are reminiscent of Mesozoic hybodont fin spines. This form does not seem close to *Sphenacanthus*. A spine from the Seminole Formation of Oklahoma was said to be reminiscent of *C. buttersi* by Zidek (1977, p. 153).

"*Ctenacanthus buttersi* St. John and Worthen"; (in) Caster (1930, p. 100), a typographical error for *C. buttersi* (see above).

Ctenacanthus cannaliratus St. John and Worthen (1883, p. 239, pl. XXI, fig. 3).

Type specimen, University of Illinois X-391, Mississippian, Chester Limestone, Chester, Illinois.

COMMENTS: The fragment upon which this species is based differs from *Acondylacanthus*

gracillimus only in the greater delicacy of its costae and tubercles, and *C. cannaliratus* is considered synonymous with *A. gracillimus* (see also *C. gracillimus*, below).

Ctenacanthus chemungensis Eastman (1907, p. 77, pl. 7, fig. 3).

Devonian, Chemung Group, Bradford Co., Pennsylvania.

COMMENTS: The species was originally named by Claypole (1885, p. 490). Eastman (1907) figured a detail of ornament from an unspecified specimen (reproduced by Caster, 1930, pl. 56, fig. 9), and no type specimen was designated; from the literature it ought to be one of the specimens collected by Beecher and deposited at New Haven or Cambridge. Eastman (1907) referred to additional specimens collected in New York; see also Caster (1930, p. 102).

Ctenacanthus clarkii Newberry (1889, p. 168, pl. XXVI, figs. 2, 3).

Type specimen, AMNH 220G, Cleveland Shale, Berea, Ohio.

COMMENTS: See also Hussakof (1908). A partial skeleton, with teeth, jaws, pectoral fins, shagreen and part of the impression of a fin-spine was referred to *C. clarkii* by Dean (1909). According to Maisey (1981) Dean's specimen should more correctly be referred to *C. compressus*, but *C. clarkii* and *C. compressus* are retained in the genus as separate species.

Ctenacanthus cliftonensis Branson and Mehl (1938, p. 122, pl. 37, figs. 16–19).

Type specimen, University of Missouri, 752 VP, lower Mississippian, Chouteau Limestone, Clifton City, Missouri.

COMMENTS: This form is similar to *C. varians*, but is provisionally retained as a separate species of *Ctenacanthus* (Maisey, 1981).

Ctenacanthus compressus Newberry (1889, p. 168, pl. XXII, fig. 4).

Type specimen, AMNH 140G, Cleveland Shale, Sheffield, Lorain Co., Ohio.

COMMENTS: The species was first named and briefly described some years earlier (Newberry, 1878, p. 191), but it was not figured in that work. The figure appearing in 1889 is reversed. See also Hussakof (1908). The type and other specimens are figured by

Maisey (1981), who also included Dean's (1909) specimen of "*C. clarkii*" in the present species, which is retained in the genus.

Ctenacanthus ? costatus Newberry and Worthen (1866, p. 120, pl. XII, fig. 5).

Mississippian, St. Louis Limestone, St. Louis, Missouri.

COMMENTS: The broad, smooth and heavily enameled costae of the type specimen are atypical of *Ctenacanthus* finspines. Subsequently this form was made the type species of *Eunemacanthus* (St. John and Worthen, 1883, p. 246, pl. XXIII, fig. 2; see also Maisey, 1982).

Ctenacanthus costellatus Traquair (1884, p. 3, pl. II).

Type specimen, BM(NH) P5900, Mississippian, Calciferous Sandstone, Dumfriesshire, Scotland.

COMMENTS: This species is known from a complete, articulated specimen, subsequently described by Moy-Thomas (1936, p. 761). Its finspines do not agree with those of *Ctenacanthus*, however, and the species has been referred provisionally to *Sphenacanthus* (Woodward, 1889; Maisey, 1982).

Ctenacanthus coxianus St. John and Worthen (1883, p. 233, pl. XXI, fig. 1).

Type specimen, USNM 13502, Mississippian, Keokuk Limestone, Montrose, Iowa; plesiotype, MCZ 5188.

COMMENTS: Eastman (1902, p. 87) noted considerable resemblance between finspines of this species and those of *C. fuscicarinatus*, and they may be closely related. An almost complete fin-spine, AMNH 11201 (Linney Coll.), lacking only the apex was collected supposedly from the Waverly Series, Marion Co., Kentucky.

Ctenacanthus crenatus McCoy (1855, p. 624, pl. 3.I., fig. 31).

Mississippian, Carboniferous Limestone, Armagh.

COMMENTS: According to McCoy (1855) and Davis (1883), this species is the same as that named *C. crenulatus* by Agassiz (1837, vol. III, p. 177, name only). McCoy's (1855) figure was reproduced by Davis (1883, pl. XLV, fig. 6), but was reversed. Davis noted that the type specimen (a fragment of spine)

was lost; it has never been relocated. Both species, *C. crenatus* and *C. crenulatus* should therefore be declared *nomina nuda*.

Ctenacanthus crenulatus Agassiz (1837, vol. III, p. 177; name only).

See *C. crenatus* (above).

Ctenacanthus cylindricus Newberry (1889, p. 202, pl. XXVI, fig. 1).

Type specimen, AMNH 358G, "Subcarboniferous," Keokuk Group, Casey Co., Kentucky.

COMMENTS: It is doubtful whether this species is based on a median (unpaired) spine. In transverse section and style or ornamentation the spine resembles those of *Gyracanthus*, except that the costae are less strongly arranged into chevrons. I do not regard this as a *Ctenacanthus* species.

Ctenacanthus decussatus Eastman (1902, p. 84, pl. 6, fig. 2, text-fig. 11).

Type specimen, USNM 4846, Mississippian, Kinderhook Limestone, location uncertain (Iowa or Illinois).

COMMENTS: The type specimen resembles that of *C. buttersi*, but not *C. pellensis* (cf. Eastman, 1902). Its ornamentation pattern, in my view, precludes it from the genus *Ctenacanthus*.

Ctenacanthus deflexus St. John and Worthen (1883, p. 234, pl. XXII, fig. 1).

Mississippian, St. Louis Limestone, Alton, Illinois.

COMMENTS: St. John and Worthen (1883) regarded this species as being allied to *C. speciosus*, which is itself probably synonymous with *C. varians* (Eastman, 1902; Maisey, 1981). Maisey (1981) retained them as separate species within the genus *Ctenacanthus*, but suggested that *C. deflexus* may be synonymous with *C. major*.

Ctenacanthus deliculatus (Eastman), Denison (1979, p. 52).

COMMENTS: The species was removed from *Homacanthus* by Denison, who suggested that it may instead pertain to *Ctenacanthus*. See Eastman (1903, p. 218, pl. III, fig. 28, and pl. V, fig. 59). The holotype of *H. deliculatus* is MCZ 5126. It is not referable to *Ctenacanthus* however, and its affinities are uncertain.

Ctenacanthus denticulatus McCoy (1855, p. 625, pl. 3K, fig. 16).

Mississippian, Carboniferous Limestone, Armagh and Drumlish (Northern Ireland), Shropshire, England.

COMMENTS: The species was named but not figured by McCoy (1848, p. 116). See also Davis (1883, p. 338, pl. XLIV, fig. 4) and Maisey (1981, fig. 8F, G). It is retained in *Ctenacanthus* by Maisey (1981).

Ctenacanthus depressus Newberry (1897, p. 291, pl. XXII, fig. 6).

Mississippian, Kinderhook Group, Le Grand, Iowa.

COMMENTS: This form may be close to *C. buttersi*, as Newberry (1897) suggested. Its smooth ornamentation pattern seems to preclude it from the genus *Ctenacanthus*, and it may be closer to *Sphenacanthus*.

Ctenacanthus distans McCoy (1855, p. 625, pl. 3K, fig. 15).

Mississippian, "red limestone" of Armagh, Northern Ireland.

COMMENTS: These elongate, slender spines resemble those of *C. formosus*, but more particularly those of *Acondylacanthus gracillimus*. Originally named but not figured by McCoy (1848, p. 116), the species was subsequently transferred to *Acondylacanthus* by Davis (1883, p. 349) and Woodward (1891, p. 108).

Ctenacanthus dubius Davis (1883, p. 340, pl. XLIV, fig. 7).

Type specimen, BM(NH) P2530, Mississippian, "Mountain Limestone" of Armagh, Northern Ireland.

COMMENTS: This species is founded on a badly crushed and distorted finspine. Its ornamentation is atypical of *Ctenacanthus* and the species is provisionally referred to *Ame-lacanthus* (see Maisey, 1982).

Ctenacanthus elegans Tuomey (1858, p. 38, woodcut, fig. A).

Devonian; base of Chattanooga Shale, Shoal Creek, nr. Florence, Lauderdale Co., Alabama.

COMMENTS: Apparently referable to *Ctenacanthus* (Tuomey suggested that "it may turn out to be identical with *C. tenuistriatus*"). Unfortunately, the type specimen is now lost.

I am indebted to Dr. Charles Copeland (Geological Survey of Alabama) for information concerning this specimen. It was probably of late Devonian rather than Mississippian age as thought by Tuomey. Apparently all of Tuomey's records and specimens were lost sometime between his death (1857) and the appointment in 1873 of his successor. During this interim the University of Alabama campus was destroyed by the 2nd Michigan Cavalry (April 4 and 5, 1865), and the type specimen is unlikely to have survived!

Ctenacanthus? erectus v. Koenen (1895, p. 3).

Upper Devonian, Büdesheim bei Gerolstein.

COMMENTS: According to Gross (1933, p. 65) this finspine has ornament like that of *Onchus curvatus* from the upper Silurian. The species may therefore represent an acanthodian, and is not regarded here as a member of *Ctenacanthus*. The specimen has not been figured.

Ctenacanthus excavatus St. John and Worthen (1875, p. 428, pl. XV, figs. 4, 5).

Mississippian, Iowa and Missouri.

COMMENTS: The species is founded upon the apical fragments of two finspines (possibly juvenile). It is difficult to assign these pieces to *Ctenacanthus*; they could represent small *Eunemacanthus* finspines (see *C. costatus*).

Ctenacanthus? fallax Leidy (1857, pl. V, fig. 30).

Type specimen, Museum of the Academy of Sciences, Philadelphia, no. 7798. Mississippian, St. Louis Limestone, St. Louis, Missouri.

COMMENTS: "founded on an indeterminate fossil" (Woodward, 1891, p. 105). How true! Illustrated but not named or described by Leidy (1857). See Gillette and Shapiro (1978, p. 116).

Ctenacanthus formosus Newberry (1873, p. 328, pl. 36, fig. 2).

Holotype, AMNH 11544, Famennian, Waverly Series, Vanceburg, Kentucky; also Berea Grit and Cuyahoga Shale (e.g., AMNH 221, 223) of Ohio.

COMMENTS: A species easily recognized by

its long, elegant slender finspines. See also Newberry (1875, p. 53, pl. LIX, fig. 1). Not listed as a member of *Ctenacanthus* by Maisey (1981) but probably close to this genus. The holotype was lost for many years, but through the endeavors of Robert Hook (University of Kentucky) it has recently been relocated (March 1983) along with a significant part of the original William Patterson collection (formerly University of Kentucky UK 1004 = M2060). The holotype has now been transferred to the American Museum of Natural History (see designation above).

Ctenacanthus furcicarinatus Newberry (1875, p. 54, pl. LIX, fig. 2).

Type specimen, AMNH 11543, Famennian, Waverly Black Shale, Vanceburg, Kentucky.

COMMENTS: The finspine ornamentation pattern is atypical for *Ctenacanthus*. The species is of considerable interest, since its finspines were found in association with teeth of "*Orodus variabilis*" and pieces of shagreen with a regular, gridlike squamation pattern of ridged scales, e.g., AMNH 409. Newberry (1875) also mentioned that fairly complete sharks had once been found by quarrymen but none of these specimens has ever been described. The holotypes of *C. furcicarinatus* and *O. variabilis*, together with a tail of a shark mentioned by Newberry (1875) as possibly pertaining to *C. furcicarinatus* have been rediscovered (1983) by Robert Hook and transferred to the American Museum.

Ctenacanthus gemmatus St. John and Worthen (1875, p. 429, pl. XV, figs. 9, 10).

Mississippian, St. Louis Limestone, Alton, Illinois.

COMMENTS: Species is probably referable to *Acondylacanthus*; it is fairly similar to *A. occidentalis*.

Ctenacanthus gemündensis Gross (1933, p. 64, pl. II, fig. 8).

Type specimen, Geologische Landesanstalt, Berlin.

Late Devonian, Schliedener Schichten, Gemünd (Eifel).

COMMENTS: An indeterminate finspine founded on very fragmentary material. Ornament pattern atypical of *Ctenacanthus*; may be an acanthodian finspine; referred to *No-*

dacosta, Gross (1940) by Denison (1975, p. 53). The type specimen was apparently destroyed in World War II (Dr. K. Fischer, personal commun.).

Ctenacanthus gondwanus Silva Santos (1947, p. 248, pl. 1, figs. 1–5).

Type specimen, National Geological Museum, Brazil, DGM 73-P. Pennsylvanian, Tubarao Series, Rio do Sul, S. Catarina, Brazil.

COMMENTS: The type specimen is the impression of a complete finspine in sandstone. Its ornamentation is atypical of *Ctenacanthus* finspines and the species probably does not belong in this genus; it may be referable to *Sphenacanthus*.

Ctenacanthus gracillimus Newberry and Worthen (1866, p. 126, pl. XIII, fig. 3).

Plesiotype, Museum of Comparative Zoology, Harvard, MCZ 5184; Mississippian, St. Louis Formation, St. Louis, Missouri; also from Alton, Illinois and Grand Rapids, Michigan.

COMMENTS: The validity of this species has been argued over since its inception. Newberry and Worthen (1866, p. 116, pl. XII, fig. 2) described another, much abraded finspine, as the type of *Leptacanthus occidentalis*. This species was subsequently referred to *Acondylacanthus*, and *C. gracillimus* was made synonymous with *A. occidentalis* (St. John and Worthen, 1875, p. 433). Later, however (St. John and Worthen, 1883, p. 238), it was decided that preference should be given to the name which was open to least doubt, and the name *C. gracillimus* was therefore used. Newberry (1889, p. 206) preferred to continue using the name *A. occidentalis*. Eastman (1902, p. 85) followed St. John and Worthen (1883) in regarding *gracillimus* as the more suitable specific name, but agreed with Newberry (1889) that this species should be referred to *Acondylacanthus*. Hussakof (1908) also used the name *A. gracillimus*. Zidek (1976) referred a finspine from the upper Mississippian of Oklahoma to *Ctenacanthus* aff. *C. gracillimus*.

There is little doubt that *C. gracillimus* should more correctly be referred to *Acondylacanthus*. The question of synonymy with *A. occidentalis* cannot be resolved since that

species is founded on indeterminate material. Elsewhere in the present work I have made certain species synonymous with *A. gracillimus* rather than with *A. occidentalis*, which to all intents can be left as a separate, indeterminate species. See also *C. cannaliratus*.

The *Ctenacanthus* sp. finspine of Kulczycki (1957, pl. XIII, fig. 2) may be referable to *A. gracillimus*.

"*Ctenacanthus gradacostata* St. John and Worth." (in) Caster (1930, p. 101). A typographical error for *C. gradocostus* (see below).

"*Ctenacanthus gradocostatus* St. J. and W." (in) Miller (1889) and Eastman (1907, p. 156). A typographical error for *C. gradocostus* (see below).

Ctenacanthus gradocostus St. John and Worthen (1875, p. 425, pl. XV, figs. 2, 3).

Syntype, University of Illinois, X-358. Mississippian, Burlington Limestone, Quincy, Illinois, Louisa Co., Indiana.

COMMENTS: Said by St. John and Worthen (1875) to "intimately" resemble *C. burlingtonensis* apart from minor differences in the ornamentation. Although similar in general shape to *Acondylacanthus* finspines, *C. gradocostus* may represent a different, allied genus with more pectinate ornament. Another specimen (AMNH 1034) bears a label in Newberry's handwriting, noting similarities with "the type."

Ctenacanthus gurleyi Newberry (1897, p. 290).

Mississippian, St. Louis Limestone, Salem, Indiana (Gurley Coll.).

COMMENTS: No type specimen is known, nor was any specimen figured. These are sufficient grounds to declare this species a *nomen nudum*, and it has elsewhere been suggested that it is synonymous with the type species, *Ctenacanthus major* (Maisey, 1981).

Ctenacanthus harrissi Caster (1930, p. 103, pl. 57, fig. 1).

Mississippian, Mt. Jewett, Pennsylvania.

COMMENTS: Caster (1930) suggests that *C. harrissi* finspines resemble those of *C. tenuistriatus* in the number of ribs and shape of tubercles. This species is provisionally retained in *Ctenacanthus* although it was not listed by Maisey (1981).

Ctenacanthus harrisoni St. John and Worthen (1883, p. 236, pl. XXIII, fig. 1).

Type specimen, (?) USNM 13505, Mississippian, St. Louis Limestone, Alton, Illinois.

COMMENTS: See also Maisey (1981, fig. 6) where the species is retained in *Ctenacanthus* as a possible synonym of *C. major*. Newberry (1889) noted similarities to *C. littoni*. See also Zidek (1977, p. 153, fig. 1B).

Ctenacanthus heterogyrus McCoy (1855, p. 625, pl. 3 I, fig. 32).

Mississippian, Carboniferous Limestone Series, Armagh, Northern Ireland; Tournai, Belgium.

COMMENTS: First mentioned by Agassiz (1837, vol. III, p. 177, name only), see also DeKoninck (1878, p. 66, pl. VII, fig. 3), Davis (1883, p. 336, pl. XLIV, figs. 1-3), Woodward (1891, p. 101), Maisey (1982, p. 11, fig. 7). The type specimen of *C. dubius* was listed under *C. heterogyrus* by Woodward (1891, p. 101). According to Khabakov (1928, p. 28, pl. IV, figs. 1-3) *C. venator* is similar to *C. heterogyrus*; this suggestion was provisionally accepted by Maisey (1982) pending examination of *C. venator*, but it seems possible that *C. venator* is actually referable to *Sphenacanthus*. *Ctenacanthus heterogyrus* was transferred to *Eunemacanthus* by Maisey (1982).

Ctenacanthus hybodontes Egerton (1853, p. 280, pl. XII).

Plesiotype, MCZ 5206 (formerly MCZ 4213), plesiotype from Mississippian coal measures of Glasgow, Scotland, also widespread in British Pennsylvanian coal measures.

COMMENTS: See also Thomson (1874), Woodward (1889), Maisey (1982). The type specimen of *C. nodosus* was referred to this species by Woodward (1889) although they are again separated by Maisey (1982). Thomson (1869) incorrectly referred spines of this species to *C. major* (the type species), and reported an associated find of finspines with a partial dentition of *Cladodus mirabilis* (see also T. P. Barkas, 1873, pp. 19, 21; Thomson, 1874). Subsequently W. J. Barkas (1874, 1878) referred these finspines to *Hybodus* and recommended suppression of the genus *Ctenacanthus*. Woodward (1889) first referred the

species to *Sphenacanthus*, though for very unsatisfactory reasons. Nevertheless, Maisey (1982) retains the species in *Sphenacanthus* on other criteria. The type specimen of *C. marshi* is very similar to *S. serrulatus* finspines.

Ctenacanthus ianishkevskyi Khabakov (1928, p. 23, pl. III, figs. 5-10).

Holotype, CNIGR 2421/2, Leningrad; Mississippian (Carboniferous Limestone C), Kuznetsk basin, Siberia.

COMMENTS: Quite atypical for *Ctenacanthus*, the species has been transferred to *Bythiacanthus* by Maisey (1982). The closest North American forms are *C. solidus* and *C. lucasi* (also transferred to *Bythiacanthus*).

Ctenacanthus jaekeli Gross (1933, p. 64, pl. II, fig. 9).

Type specimen, Geologisch-Paläontologisches Museum, Berlin; Upper Devonian, Wildungen.

COMMENTS: Gross (1933) noted similarities between this form and *Euphyacanthus semistriatus* Traquair (1894); this in turn resembles *Tristychius* in its finspine morphology (Dick, 1978). Referred to *Homacanthus* and regarded as an acanthodian by Denison (1979, p. 52). The type specimen is unfortunately now lost, probably as a result of bombing in World War II (Dr. K. Fischer, personal commun.).

Ctenacanthus keokuk St. John and Worthen (1875, p. 427, pl. XV, fig. 8).

Type specimen (?), USNM 418, Mississippian, Keokuk Limestone, Boonville, Missouri.

COMMENTS: Supposed type specimen does not agree with figures, which may be composites. Probably referable to *Acondylacanthus*.

Ctenacanthus laevis Davis (1883, p. 341, pl. XLV, fig. 1).

Type specimen, BM(NH) P2531, Mississippian, Carboniferous Limestone, Armagh.

COMMENTS: Woodward (1891, p. 102) suggested that the species pertains to *Acondylacanthus*, but the ornamentation and shape of their finspines disagree. Placed in a new genus, *Amelacanthus*, by Maisey (1982).

Ctenacanthus lamborni Wells (1944, p. 65, pl. 1, figs. 1–6).

Type specimen, Ohio State University Geological Museum No. 19501, upper Pennsylvanian, Ames Limestone, Guernsey Co., Ohio.

COMMENTS: According to Wells (1944), at least two previously described specimens referred to *C. amblyxiphias* actually pertain to *C. lamborni* (in Eastman, 1903, and Branson, 1916). A finspine like that of *C. lamborni* was found associated with a toothplate of *Megactenopetalus kaibabanus* (see Hansen, 1978, figs. 3–6).

Ctenacanthus latispinosus Whiteaves (1881, p. 99).

Lower Devonian, Campbellton, New Brunswick.

COMMENTS: See also Whiteaves (1889, p. 95, pl. X, fig. 3). Referred to the acanthodian genus *Climatius* by Woodward (1889, p. 183; 1891, p. 33), and Denison (1979, p. 25).

Ctenacanthus limaformis Davis (1883, p. 339, pl. XLIV, fig. 5).

Type specimen, BM(NH) P2535, Mississippian, Carboniferous Limestone, Bristol, England.

COMMENTS: The type specimen is a badly damaged finspine. The preserved ornament is reminiscent of *C. vetustus*, but it is unlikely that either species is referable to *Ctenacanthus*.

Ctenacanthus littoni Newberry (1889, p. 201, pl. XXV, fig. 3).

Type specimen, AMNH 1050 (G), Mississippian, St. Louis Limestone, St. Louis, Missouri.

COMMENTS: See also Hussakof (1908) and Maisey (1981), who retain the species in *Ctenacanthus*. Newberry (1889) noted similarity with *C. harrisoni*.

Ctenacanthus longinodosus Eastman (1902, p. 78, text-fig. 8, pl. 5, fig. 2).

Paratypes, MCZ 5182 and USNM 3393, Mississippian, "derived from the Kinderhook Limestone," probably near Burlington, Iowa ("North hill exposure").

COMMENTS: Eastman (1902) noted a resemblance between the type specimen and spines of *Oracanthus*, *Glymmatacanthus*

rudis and *Batacanthus baculiformis*. While their ornamentation patterns are similar, however, the forms of the spines are rather different. The affinities of *C. longinodosus* are obscure, but it does not seem referable to *Ctenacanthus*.

Ctenacanthus lucasi Eastman (1902, p. 80, pl. 6, fig. 1, text-fig. 9).

Type specimen, USNM 4844, Mississippian, Kinderhook Limestone, Iowa.

COMMENTS: Another specimen, USNM 4686, is referred to this species. Maisey (1982) transfers the species to *Bythiacanthus*.

Ctenacanthus magnus (in) Thomson (1874, p. 59).

COMMENTS: This is an invalid name. In an earlier publication, Thomson (1869, p. 102) referred a specimen to *Ctenacanthus major*. The specimen was reassigned to *C. hybodontoides* by Thomson (1874), but in a footnote (p. 59) he incorrectly cited the previous identification as *C. magnus*. *Ctenacanthus magnus* must therefore be regarded as an invalid junior synonym of *Sphenacanthus hybodontoides*.

Ctenacanthus major Agassiz (1837, vol. III, p. 10, table 4).

Type specimen, City of Bristol Museum No. C4152, Mississippian, Carboniferous Limestone Series, Avon Gorge, Bristol (widespread distribution recorded elsewhere).

COMMENTS: The type species of *Ctenacanthus*. See also Davis (1883, p. 334, plate XLII, figs. 1, 2), Maisey (1981, figs. 1, 10L). Specimens referred to this species by Trautschold (1874a, 1874b) are cephalopods (Khabakov, 1928). Thomson (1869, p. 102) referred a *Sphenacanthus* finspine to *C. major* (Woodward, 1889, p. 242), as did Newberry (1873; see Maisey, 1981, 1982). The following species were regarded as synonyms of *C. major* by Woodward (1891) and Maisey (1981): *C. tenuistriatus*, *C. maximus* and *C. salopiensis*. In addition, Maisey (1981) suggested that the following species may be synonymous with *C. major*: *C. varians*, *C. varians* var. *russakovi*, *C. speciosus*, *C. spectabilis*, *C. harrisoni*, and *C. deflexus*.

Ctenacanthus maranhensis Silva Santos (1946, p. 282, pl. 1, figs. 1, 2).

Type specimen, DGM 448-P, National Geological Museum, Brazil. Lower Permian, Formação Pedra do Fogo, Maranhão, Brazil.

COMMENTS: The species is based on a fragment of finspine which, from its shape in transverse section and ornamentation pattern, is not referable to *Ctenacanthus*. Instead it may be closer to *Sphenacanthus* or to *Wodnika*.

Ctenacanthus marshi Newberry (1873, p. 326, pl. XXXVI, fig. 3).

Type specimen, YPM 2873, Pennsylvanian, Coal Measures, Lanesville.

COMMENTS: Referred to *Sphenacanthus* by Maisey (1982); the type specimen of *C. marshi* closely resembles *S. hybodontoides* and *S. serrulatus* finspines.

Ctenacanthus maximus De Koninck (1878, p. 68, pl. VII, fig. 1).

Type specimen, IRSNB P1305, Mississippian, Carboniferous Limestone, Soignies, Belgium.

COMMENTS: Generally regarded as a synonym of *C. major*, the type species (Davis, 1883; Woodward, 1891; Maisey, 1981).

Ctenacanthus mayi Newberry and Worthen (1870, p. 372, pl. II, fig. 2).

Type specimen, University of Illinois, X-1166, Mississippian, "lower Carboniferous Limestone," Burlington, Iowa.

COMMENTS: The ornament pattern and shape of the finspine in transverse section seem to preclude this species from *Ctenacanthus*, but its affinities are obscure. Another specimen, USNM 14184, represents the lower part of a similar finspine, with a very deep transverse section, not unlike some *Bythiacanthus* finspines.

Ctenacanthus minor Davis (1879b, p. 531, with fig.).

Pennsylvanian, lower Coal Measures (Black-Bed Coal), near Bradford, Yorkshire, England.

COMMENTS: The type specimen is very small and does not seem to be fully formed. It may therefore pertain to a juvenile individual, probably of *Sphenacanthus* (Woodward, 1889, p. 244; Maisey, 1982, p. 19).

Ctenacanthus mutabilis Branson (1933, p. 180, fig. 1, nos. 13, 14).

Triassic, middle Phosphoria Formation, Wind River Mountains, Wyoming.

COMMENTS: This species is based on an indeterminate fragment of a finspine. The "ridges" noted by Branson appear to be no more than areas in between grooves for vascular canals. The only ornament is an enameled area on the presumed anterior margin. This is reminiscent of *Nemacanthus*, and it may be that *C. mutabilis* is an early neosealachian. It is not referable to *Ctenacanthus*.

Ctenacanthus nodocostatus Hussakof and Bryant (1918, p. 159, pl. 51, fig. 1).

Type specimen, Buffalo Museum, E2083, upper Devonian, Catskill Formation, "Second Mountain Sandstone," Venango County, Pennsylvania.

COMMENTS: See also Maisey (1981, fig. 10K) where the species is retained in *Ctenacanthus*.

Ctenacanthus obscuracostatus Branson (1916, p. 654, pl. IV, fig. 2, text-figs. 2, 3).

Type specimen, University of Missouri, No. 710, Permo-Carboniferous, lower Embury Formation, Big Popo Agie Canyon, Wyoming.

COMMENTS: An indeterminate species based on a finspine that resembles those of *Acondylacanthus* more than those of *Ctenacanthus*.

Ctenacanthus ornatus Agassiz (1837, p. 12, pl. II, fig. 1).

Devonian, Old Red Sandstone.

COMMENTS: Generally considered to be based on a fragment of climatiiform acanthodian spine, and referred to *Climatius*; see also Woodward (1891, p. 32), Pageau (1969, p. 455, fig. 16), Denison (1979, p. 25).

Ctenacanthus panderi (Eichwald): Woodward (1889, p. 306).

Mississippian, Carboniferous Limestone, Toulou, U.S.S.R.

COMMENTS: Originally referred to *Hybodus* (Eichwald, 1860, p. 1603), the species is "founded upon a spine probably of *Ctenacanthus*" (Woodward, 1889, p. 306). This is unhelpful, however, as Woodward's concept of *Ctenacanthus* spines was rather broad. Interestingly, it was not subsequently included

in Woodward's (1891) list of *Ctenacanthus* species.

Ctenacanthus parvulus Newberry (1875, p. 55, pl. LIX, fig. 3).

Upper Devonian, Cleveland Shale, Bedford, Ohio.

COMMENTS: Newberry (1875) referred this species (which seems to be based on an immature spine) to *Ctenacanthus* with misgivings. It has subsequently been referred to *Hoplonchus* (Newberry, 1889, p. 169; Woodward, 1891, p. 107; Hussakof, 1908, p. 49; Denison, 1979, p. 52). It is possible, however, that the species is founded on a juvenile *Ctenacanthus* fin spine, since the tip of a similar spine is present on AMNH 189 (the articulated *Ctenacanthus* described by Dean, 1909).

Ctenacanthus pellensis St. John and Worthen (1883, p. 237, pl. XXI, fig. 2).

Type specimen, USNM 13514, Mississippian, St. Louis Formation, Pella, Iowa.

COMMENTS: This species is founded on a small fragment of fin spine which closely resembles the type specimen of *C. venustus*. The two species may therefore be synonymous, and *C. pellensis* is retained in *Ctenacanthus* here although it was not listed previously (Maisey, 1981). Another fragment was described and figured by Branson (1906, p. 1393, fig. 25), from the Salem Limestone of Salem, Indiana.

Ctenacanthus peregrinus Khabakov (1928, p. 25, pl. III, figs. 1-4).

Holotype, CNIGR 2421/3, Leningrad, Carboniferous Limestone, C₁ zone (Tournaian), Roika Village, Tom River, Siberia.

COMMENTS: The strong pustulose ornament of the figured specimen is reminiscent of *Bythiacanthus*; see Maisey (1982, fig. 3C-F).

Ctenacanthus plicatus Davis (1883, p. 342, pl. XLV, fig. 4).

Mississippian, "Mountain Limestone," Armagh, Northern Ireland.

COMMENTS: First listed as *Onchus plicatus* (Agassiz, 1843, vol. III, p. 177, name only). Referred to a new genus, *Amelacanthus*, by Maisey (1982, fig. 5F-I).

Ctenacanthus pugiunculus St. John and Worthen (1875, p. 430, pl. XXI, fig. 9).

Type specimen, USNM 13525, Mississippian, St. Louis Limestone, St. Louis, Missouri.

COMMENTS: The type specimen is a long, slender spine. It does not resemble the stout, heavily tuberculate spine referred to this species by Newberry (1897, p. 288, pl. XXII, fig. 4). His view that the species pertains to *Oracanthus* seems untenable (see also Denison, 1979, p. 36). It is probably not referable to *Ctenacanthus*, however, but may be allied to *Asteroptychius*. Another specimen supposedly of this species (AMNH 5285) cannot be located at the time of writing. *Ctenacanthus similis* is close to the present species and the two may be synonymous.

Ctenacanthus pustulatus Davis (1883, p. 344, pl. XLV, fig. 2).

Type specimen, British Museum (Natural History) BM(NH) P2529, Mississippian, Lower Carboniferous Limestone, Armagh, Northern Ireland.

COMMENTS: Woodward (1891, p. 102) suggested that the species may pertain to *Asteroptychius*. Maisey (1982) referred it to a new genus, *Amelacanthus*.

Ctenacanthus randalli Newberry (1889, p. 105, no illustrations).

Type specimen, AMNH 6675, Frasnian, Olean conglomerate (Chemung Group), near Warren, Pennsylvania.

COMMENTS: See also Eastman (1907, p. 154), Hussakof (1908, p. 46), Caster (1930, p. 102), and Maisey (1981, p. 20, fig. 8E). Retained in *Ctenacanthus* by Maisey (1981).

Ctenacanthus rectus Davis (1883, p. 345, pl. XLV, fig. 5).

Mississippian, "Mountain Limestone," Armagh, Northern Ireland.

COMMENTS: First listed by Agassiz (1843, vol. III, p. 177, name only) as *Onchus rectus*. An indeterminate species.

Ctenacanthus salopiensis Davis (1883, p. 339, pl. XLIV, fig. 6).

Type specimen, BM(NH) P2523, Mississippian, Carboniferous Limestone, Oretton, Shropshire, England.

COMMENTS: A synonym of *C. major*, ac-

cording to Woodward (1891, p. 98) and Maisey (1981, p. 19).

Ctenacanthus sculptus St. John and Worthen (1875, p. 421, pl. XIV, fig. 1).

Type specimen, USNM 13520, Mississippian, upper Kinderhook Beds, lower (no. 1) fish bed, Burlington, Iowa.

COMMENTS: Probably close to *Ctenacanthus*, but ornament pattern is not pectinate. Nonetheless, the tubercles on the costae are arranged transversely. Tubercles become coarser anteriorly, though less strongly than in *C. vetustus*, with which *C. sculptus* may be allied. Both species may eventually be removed from the genus *Ctenacanthus*. Another specimen, USNM 6048, from St. Louis, Missouri, is referred to *C. sculptus*.

Ctenacanthus semicostatus (St. John and Worthen): Eastman (1902, p. 89).

Type specimen, MCZ 5187, Mississippian, upper Burlington Group, Burlington, Iowa.

COMMENTS: The genoholotype of *Anaclitacanthus* St. John and Worthen (1875, p. 443, pl. XVI, fig. 14). The type specimen is not a *Ctenacanthus* fin spine, and Eastman (1902) is hardly justified in his remarks that its "relations are evidently with the genus *Ctenacanthus* instead of *Anaclitacanthus*." Most probably the type specimen is a paired spine, possibly acanthodian. There are interesting similarities with *C. cylindricus*. The pectoral spines of *Lupopsyrus pygmaeus* Bernacsek and Dineley (1977), a climatiid acanthodian, are similar to the type specimen of *Anaclitacanthus*, but have fewer and coarser ridges. Also similar is *Acondylacanthus? mugdianus* of St. John and Worthen (1883, p. 244, pl. XXIV, fig. 3).

Ctenacanthus serrulatus (Agassiz): Traquair (1884, p. 6) non-Agassiz (1845, p. 119, pl. XXXIII, fig. 24).

Type specimen, RSM. GY. 1878.18.15. Calciferous sandstones (Mississippian), Burdiehouse, near Edinburgh, Scotland.

COMMENTS: This is the type species of *Sphenacanthus* Agassiz (1837, vol. III, p. 24), which Traquair (1884) regarded as a synonym of *Ctenacanthus*, although elsewhere these genera are considered distinct (e.g., Woodward, 1889, p. 242; Maisey, 1981, 1982). Spines referred to *Ctenacanthus ser-*

ruleatus by Agassiz (1845) seem to pertain to *Psammosteus meandrinus* Agassiz (1845) (see Woodward, 1891, p. 126), which has nothing to do with *Sphenacanthus*. See Agassiz (1837, vol. III, p. 24, pl. I, figs. 11–13) and Maisey (1982, fig. 8A).

Ctenacanthus similis St. John and Worthen (1875, p. 431, pl. XV, fig. 11).

Syntype, University of Illinois, X-1157, Mississippian, Chester Limestone, Chester, Illinois.

COMMENTS: This species is close to *C. pugunculus* and they may be synonymous. These elongate slender spines are not referable to *Ctenacanthus*, but have yet to be assigned to a different genus.

Ctenacanthus solidus Eastman (1902, p. 90, pl. 7, fig. 3, text-fig. 13).

Type specimen, USNM 3383, paratypes, USNM 4843, MCZ 5185, Mississippian, Kinderhook Formation, Iowa and Illinois.

COMMENTS: Eastman (1902, pl. 7, fig. 3) figured the paratype, USNM 4843, only; see Maisey (1982, fig. 3A) for the type. Eastman's text-figure 7 is misleading as the spine is much deeper than he suggests anteroposteriorly, but is damaged so that its posterior wall has broken away. The species is transferred from *Ctenacanthus* to *Bythiacanthus* by Maisey (1982). Paratype MCZ 5185 is recognizable as pertaining to this species, but has suffered from deformational shattering within the matrix.

Ctenacanthus speciosus St. John and Worthen (1875, p. 424, pl. XIV, figs. 3, 4).

Type specimen, USNM 13518, Mississippian, Kinderhook Formation, "lower fish bed," Iowa.

COMMENTS: Synonymous with *C. varians* according to Eastman (1902, p. 89). Also may be synonymous with *C. major* according to Maisey (1981, p. 19).

Ctenacanthus spectabilis St. John and Worthen (1875, p. 420, pl. XV, fig. 1).

Type specimen, USNM 13519, Mississippian, Kinderhook Beds, La Grande, Iowa.

COMMENTS: See also Eastman (1902, p. 87, pl. 5, fig. 1) and Maisey (1981, fig. 5).

Ctenacanthus sulcatus (Agassiz): Davis (1883, p. 343, pl. XLV, fig. 3).

Type specimen, Bristol City Museum, C4154, Mississippian, "Mountain Limestone," Armagh, Northern Ireland.

COMMENTS: The species was first described (as *Onchus sulcatus*) by Agassiz (1837, vol. III, p. 8, table 1, fig. 6). Included in *Ctenacanthus* by Davis (1883) and Woodward (1891), but made the type species of a new genus, *Amelacanthus*, by Maisey (1982).

Ctenacanthus tenuirostris von Meyer (1854, p. 53, pl. VIII, figs. 18, 19, 20).

COMMENTS: An inadequately described species, regarded by De Koninck as identical with *C. maximus*. Apparently von Meyer was referring to *C. tenuistriatus* (see below) but got the name wrong (see also Woodward, 1891, p. 98). This is an awkward reference to retrieve, since Woodward (1891) incorrectly lists it as "Roemer, 1850." Not only was the volume published in 1854 (Roemer's contribution being delivered in 1850), but von Meyer actually described the fish remains in that work (pp. 53–54). Von Meyer suggests that some teeth resembling those of "*Dicrenodus*" or "*Carcharopsis*" may have pertained to *C. tenuistriatus*, which is founded upon a fragmentary spine having *Ctenacanthus*-like ornamentation.

Ctenacanthus tenuistriatus Agassiz (1837, vol. III, p. 11, table 3, figs. 7–11).

Paratypes, BM(NH) P495, 2225, Bristol City Museum (no catalogue number, now lost). Mississippian, "Mountain Limestone," Bristol.

COMMENTS: See also De Koninck (1878, p. 67, pl. VII, fig. 2), Davis (1883, p. 335, pl. XLIII, figs. 1, 2), Maisey (1982, fig. 3). Regarded as a synonym of *C. major* by Woodward (1891, p. 98) and Maisey (1981, p. 19).

Ctenacanthus triangularis Newberry (1873, p. 329, pl. XXXVI, fig. 1).

Type (?) specimen (cast), AMNH 423 (G), Mississippian, Waverly Series, Oil Creek, Pennsylvania.

COMMENTS: The wax cast AMNH 423 (G) agrees with Newberry's (1873) published figure. The whereabouts of the natural mould is unknown. Said to have been collected in association with teeth like those of *Orodus* and *Psammodus*. Finspine ornament is atyp-

ical of *Ctenacanthus*, but is like that of *Wodnika*.

Ctenacanthus varians St. John and Worthen (1875, p. 422, pl. XIV, fig. 2).

Type specimen, MCZ 5186, Mississippian, Kinderhook Series, "upper fish bed," Flint River, near Burlington, Iowa.

COMMENTS: See also Eastman (1902, p. 89), Maisey (1981, fig. 4). See *C. speciosus*, which is probably synonymous. The present species may be synonymous with *C. major* (Maisey, 1981, p. 19).

Ctenacanthus varians St. John and Worthen var. *russakovi* Khabakov (1928, p. 26, pl. IV, figs. 11–14).

Holotype, CNIGR 2421/1, Leningrad, Lower Carboniferous, C₁ zone, Kirghizian Steppes, Siberia.

COMMENTS: May be synonymous with *C. major* (Maisey, 1981, p. 19).

Ctenacanthus near *C. varians* St. John and Worthen: Dorr and Moser (1964, p. 108, figs. 1–5).

Mid-Mississippian, Michigan Formation, Grand Rapids, Michigan: UMMP 45738.

COMMENTS: Seems to resemble the type specimen quite closely. Associated with coprolite pellets.

Ctenacanthus venator Khabakov (1928, p. 28, pl. IV, figs. 1–3).

Mississippian, C₁–C₂ zones, Donetsk Basin, Lissichia Balka.

COMMENTS: Said by Khabakov (1928) to resemble *C. heterogyrus*, the figured specimen bears a clear resemblance to *Sphenacanthus*; see also Maisey (1982, fig. 7J–M). The holotype is apparently lost (O. Lebedev, personal commun., May 1982).

Ctenacanthus venustus Eastman (1902, p. 81, pl. 3, fig. 2, text-fig. 10).

Holotype, MCZ 5183, plesiotype USNM 3385, Mississippian, Kinderhook Group, ?Iowa.

COMMENTS: Eastman (1902) figured the plesiotype. This and the holotype are figured by Maisey (1981, fig. 10A–J). Other referred specimens are USNM 4684 and USNM 3381 (two specimens). The species was retained in *Ctenacanthus* by Maisey (1981).

Ctenacanthus vetustus Newberry (1873, p. 326, pl. XXXV, fig. 3).

Type specimen, AMNH 351, Upper Devonian, Cleveland Shale, Sheffield Township, Lorain Co., Ohio.

COMMENTS: See also Newberry (1889, pl. XXVIII, fig. 5), Hussakof (1908, p. 46). Finspines associated with *Orodus variabilis* teeth in CMNH 8103A, 8103B, and assigned to a new, but as yet undescribed, genus (Hlavin, 1972, 1976).

Ctenacanthus wrightii Newberry (1884, p. 206, pl. XVI, figs. 12–14).

Type specimen, AMNH 352, Middle Devonian (Erian), Moscow Shale, Hamilton Group, Yates Co., New York.

COMMENTS: See also Newberry (1889, p. 66, pl. XXVI, fig. 4), Eastman (1907, p. 153), Hussakof (1908, p. 46), Hussakof and Bryant (1918, p. 161, pl. 52, fig. 2). Spelt *wrightii* by all but Newberry (1884, 1889).

Ctenacanthus? xiphias St. John and Worthen (1883, p. 244, pl. XVI, fig. 1).

Type (?) specimen, USNM 3391, Mississippian, Keokuk Limestone, Keokuk Rapids, near Keokuk, Iowa.

COMMENTS: Founded on an abraded and worn specimen, this indeterminate species was referred tentatively to *Acondylacanthus* by St. John and Worthen (1883). In shape and overall form, however, the type (?) specimen seems more like a *Ctenacanthus* fin-spine (see also Eastman, 1902, p. 86).

REFERENCES TO *Ctenacanthus*, SPECIES INDETERMINATE

The following references are arranged chronologically.

Ctenacanthus sp. (Davis, 1876, p. 335, no. 4), probably *Sphenacanthus*.

Ctenacanthus sp. (Davis, 1876, p. 335, no. 5), probably *Sphenacanthus*.

Ctenacanthus sp. (Eastman, 1902, p. 76), MCZ 5189, Pennsylvanian, Carlinville, Illinois; probably *Sphenacanthus*.

Ctenacanthus sp. indet. (Eastman, 1902, p. 83), USNM 3480, Mississippian, Keokuk Limestone, near Keokuk, Iowa. Close to

C. acutus; probably not referable to *Ctenacanthus*.

Ctenacanthus sp. (Hussakof and Bryant, 1918, p. 161), Buffalo Museum no. E2498, Devonian, Genesee Series, Conodont Bed, Erie Co., New York; may be a distinct species.

Ctenacanthus sp. (Branson and Mehl, 1938, p. 123, pl. 37, fig. 20). University of Missouri no. 730 VP, lower Mississippian, Chouteau Province, Missouri. An indeterminate fragment of spine, probably not referable to *Ctenacanthus*. No ornament is preserved.

Ctenacanthus sp. (Kulczycki, 1957, p. 285, pl. XIII, fig. 2), Famennian, lower *Cheiloceras* Beds, Kielce, Holy Cross Mountains, Poland. Similar to *Acondylacanthus* and resembles *C. gracillimus* except for details of ornamentation pattern.

Ctenacanthus sp. indet. (Dorr and Moser, 1964, pp. 110 and 111, pl. 1, figs. 6, 8). These specimens (UMMP 23845 and 45739) are indeterminate impressions of spines. Their ornamentation is atypical of *Ctenacanthus*.

Ctenacanthus sp. (Bendix-Almgreen and Malzahn, 1969, p. 44; see also Schaumberg, 1977, p. 308, fig. 9), may be a neoselachian. Schaumberg (1982) has referred this specimen to a new genus and species, *Hopleacanthus richelsdorfensis*, and several articulated specimens are now known from the Permian Kupferschiefer of Germany.

"*Ctenacanthus* type" (Bendix-Almgreen, 1975, p. 551), Upper Carboniferous, Greenland.

Ctenacanthus sp. (Janvier, 1977, p. 131, fig. 1C), Upper Devonian, Iran (Iran National Museum of Natural History, MMTT 5005).

"Indeterminate ctenacanthid" spines (Janvier, 1977, p. 129, fig. 1A, B); Devonian, Aroma Province, Brazil.

Ctenacanthus sp. (Zidek, 1977, p. 151, fig. 1A), Pennsylvanian, Seminole Formation, Tulsa County, Oklahoma. Said to have similarities with *C. buttersi*, but may be referable to *Sphenacanthus*.

Ctenacanthus sp. (Zidek, 1977, p. 151, fig. 1B), Pennsylvanian, Coffeyville Formation, Tulsa County, Oklahoma. Said to have similarities with *C. harrisoni*.

DISCUSSION

The following species of *Ctenacanthus* should be considered invalid:

buttersi (misspelling of *buttersi*)
crenulatus (name only—later described as *crenatus*)
fallax (indeterminable)
gradacostata (misspelling of *gradocostus*)
gradocostatus (misspelling of *gradocostus*)
gurleyi (no holotype or figure)
magnus (incorrect citation)
rectus (indeterminable)
tenuirostris (misspelling of *tenuistriatus*)
wrighti (misspelling of *wrightii*)

The type specimens of the following species are known to be lost or destroyed and no neotypes have been designated:

crenatus
elegans
gemündensis
jaekeli
venator

The following species are left as indeterminate, either because they are founded on inadequate material, or because the original descriptions are vague and imprecise, or because the material has not been examined and its whereabouts not yet established:

limaformis (badly damaged holotype)
panderi (inadequate description)
parvulus (fragment of spine apex)
xiphias (damaged holotype—no details visible)

The following species have been referred to acanthodians:

abnormis (to *Machaeracanthus*)
bohemicus (to *Machaeracanthus*)
cylindricus (resembles *Gyracanthus*)
erectus ("Onchus"?)
gemündensis (to *Nodacosta*: holotype destroyed)
latispinosus (to *Climatius*)
ornatus (to *Climatius*)
semicostatus (*Homalacanthus*; resembles *Lupopsyrus*)

Homacanthus deliculatus was referred to *Ctenacanthus* by Denison (1979), but it prob-

ably does not belong to this genus, and I consider this to be an acanthodian species. *Ctenacanthus longinodosus* may also be an acanthodian.

The following species have been, or probably should be, referred to another form-genus, *Acondylacanthus*:

browni
burlingtonensis
cannaliratus
distans
gemmatus
gracillimus
keokuk
obsucrocostatus

The following species have been, or probably should be, referred to the genus *Asteroptychius*:

bellus
pugiunculus
similis

The following species have been, or probably should be, referred to *Sphenacanthus*:

aequistriatus
costellatus
depressus
gondwanus
hybodooides
magnus (invalid—see above)
marshi
minor (juvenile)
serrulatus

The following species have been, or probably should be, referred to other genera:

acutus (resembles *Tristychius*)
bosnensis (to *Nemacanthus*)
brevis (to *Bythiacanthus*)
buttersi (hybodont?)
costatus (to *Eunemacanthus*)
dubius (to *Amelacanthus*?)
excavatus (to *Eunemacanthus*?)
gradocostus (close to *Acondylacanthus*)
heterogyus (to *Eunemacanthus*)
ianishevskiyi (to *Bythiacanthus*)
laevis (to *Amelacanthus*)
lucasi (to *Bythiacanthus*)
maranhensis (close to *Sphenacanthus* or *Wodnika*)

mayi (resembles *Bythiacanthus*)
mutabilis (resembles *Nemacanthus*)
peregrinus (resembles *Bythiacanthus*)
plicatus (to *Amelacanthus*)
pustulatus (to *Amelacanthus*)
solidus (to *Bythiacanthus*)
triangularis (hybodont?)

The following list of species still referred to *Ctenacanthus* is slightly revised from Maisey (1981):

angulatus
angustus
chemungensis
clarkii
cliftonensis
compressus
deflexus (synonym of *C. major*)
denticulatus
formosus
harrissi
harrisoni (synonym of *C. major*)
littoni
major (type species)
maximus (synonym of *C. major*)
nodocostatus
pellensis
randalli
salopiensis (synonym of *C. major*)
speciosus (synonym of *C. major*)
spectabilis (synonym of *C. major*)
tenuistriatus (synonym of *C. major*)
variens (synonym of *C. major*)
venustus

The following species are founded in fin-spines that resemble those of *Ctenacanthus* but are sufficiently different (in my view) to preclude them from that genus:

amblyxiphias (has continuous pectinate keel anteriorly)
coxianus (atypical ornament)
decussatus (atypical ornament)
furcicarinatus (atypical ornament)
lamborni (has continuous pectinate keel anteriorly)
sculptus (atypical ornament)
vetustus (atypical ornament)
wrightii (atypical ornament)

The stratigraphic distribution of the species retained in the genus *Ctenacanthus* (when all

species thought to be synonymous with *C. major* are discounted) is as follows:

Lower Carboniferous (Mississippian)—eight species.

Upper Devonian—Seven species. This is a relatively restricted geological range, whereas "*Ctenacanthus*" *sensu lato* (i.e., all the species listed here) ranges from the Lower Devonian (e.g., *C. abnormis*, *C. bohemicus*, *C. latispinosus*, all coincidentally now referred to acanthodians) to the Triassic (e.g., *C. mutabilis*, *C. bosnensis*). All the species retained in *Ctenacanthus* are from marine deposits. Only two of these species (the late Devonian *C. clarkii* and *C. compressus*) are known from articulated remains (Maisey, 1981).

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